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Matthews, Ty W.; Tyre, Andrew J.; Taylor, J. Scott; Lusk, Jeffrey J.; and Powell, Larkin A., "Greater prairie-chicken nest success and habitat selection in southeastern Nebraska" (2013). *Papers in Natural Resources*. 453.
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Published in *The Journal of Wildlife Management* 77:6 (August 2013), pp. 1202–1212; doi: 10.1002/jwmg.564
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Greater prairie-chicken nest success and habitat selection in southeastern Nebraska

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Abstract

Greater prairie-chickens (*Tympanuchus cupido pinnatus*) are reported to benefit from grasslands created through the Conservation Reserve Program (CRP). Prairie-chicken population size increased noticeably in southeastern Nebraska after >15% of county-level landscapes were converted to CRP grasslands. But, the mechanisms behind the increase in population size are not well understood, and managers and policy makers could benefit from evidence of CRP's relative contribution to populations of prairie-chickens. Therefore, our objectives were to characterize the relations of vegetation structure and composition with prairie-chicken nest-site selection and nest survival rates at both the macrohabitat (within landscape of study site) and microhabitat (at the nest) level. We radio-marked female prairie-chickens at a study site with >15% of land enrolled in CRP in Johnson County in southeastern Nebraska. We monitored 90 nests during 2006–2007, 36 (40%) of which were successful. We compared nest sites' macro- and microhabitat characteristics with random points using discrete choice analyses, and we used logistic exposure analyses to assess the effect of habitat and other variables on nest survival. Prairie-chickens were 5.70 (95% CI: 2.60–12.48) times more likely to select cool-season CRP fields, and 5.05 (95% CI: 2.17–11.72) times more likely to select warm-season CRP fields for nesting relative to selecting rangeland. Prairie-chickens selected nest sites, relative to sites available in fields selected for nesting, with abundant grass cover and moderate levels of forb cover and standing litter. Females also selected sites at upper elevations. Nest survival was influenced by macrohabitat, microhabitat, and temporal variables; nest survival was greater in CRP fields and greatest for nests with abundant grass cover and forb cover and moderate levels of residual litter. Nest survival peaked, temporally, with nests initiated in late May. The size of the prairie-chicken population in southeastern Nebraska has increased since the landscape was modified under CRP, and the reproductive benefits that our study demonstrates could support such population-level responses. We would expect the population to continue to benefit from management that provides high quality, diverse grasslands.

Keywords: *Tympanuchus cupido,* Conservation Reserve Program, grassland, greater prairie-chicken, nest survival, radio-telemetry

Greater prairie-chicken (*Tympanuchus cupido pinnatus*; hereafter prairie-chicken) population size in southeastern Nebraska prior to 1990 was extremely small because of conversion of grasslands to agricultural fields (Johnsgard 1983, Schroeder and Robb 1993). Prairie-chickens were never completely extirpated from this region, and the population began to increase noticeably following the restoration of grasslands as part of the United States Department of Agriculture's Conservation Reserve Program (CRP; Powell et al. 2011). Although prairie-chickens in southeastern Nebraska appear to have benefited from grasslands established through CRP, the mechanisms (increased survival and/or productivity) behind the increase in population size are not well understood. Our goal was to evaluate the role CRP plays in sustaining reproductive success of prairie-chickens in this region.

Nesting habitat has been cited as a major limiting factor in sustaining prairie-chicken populations (Bergerud 1988), and nest success may be affected by macrohabitat factors, such as land cover and fragmentation (McNew et al. 2011b), and microhabitat factors, such as herbaceous species composition and structure (Hamerstrom et al. 1957, Buhnerkempe et al. 1984, McKee et al. 1998). Fields enrolled in CRP in southeastern Nebraska are

commonly dominated by smooth brome (*Bromus inermus*), and Svedarsky (1979) found that prairie-chickens selected nest sites in grasslands with a similar composition. These grasslands provide large expanses of undisturbed dense cover with structure (height and density) that would appear to match needs for nest habitat (Svedarsky et al. 2003). However, whether vegetation composition remains favorable for nesting is unknown; undisturbed CRP fields may have increased litter accumulation and may lack vegetative diversity (Buhnerkempe et al. 1984, Millenbah et al. 1996, McCoy et al. 2001). Grasslands enrolled in CRP composed of native warm-season grasses and other undisturbed grasslands may have vegetation that is taller and denser than that which is used by nesting prairie-chickens (Westemeier 1973, Svedarsky et al. 2003), whereas grazed pastures and rangelands may be too short and lack sufficient residual litter (Buhnerkempe et al. 1984; Walk 2004; McNew et al. 2011a, 2011b).

Nest success is an influential factor determining annual recruitment and population stability of prairie-chickens (Horkel et al. 1978, Burger et al. 1989). Wisdom and Mills (1997) reported that nest success, along with brood survival, accounted for the largest amount of variability in population growth. Variability in nest success has been attributed to vegetation composition at the nest site including residual litter, forb, and grass cover (McKee et al. 1998). Lesser prairie-chicken (*Tympanuchus pallidicinctus*) nest survival also responded to vegetation composition and structure (Pitman et al. 2005). Habitat characteristics at larger scales may influence nest success; nests in smooth brome had greater success rates than other pasture and native grasses and wheat stubble in Illinois (reviewed by Svedarsky et al. 2003), and distance to woodland may also influence the success of nests (McKee et al. 1998). Fields et al. (2006) also found success of lesser prairie-chicken nests was negatively affected by precipitation and nest age.

We assessed selection of nesting habitat by a sample of radio-tagged prairie-chickens from a population in a landscape containing a variety of grasslands. We evaluated habitat selection at 2 spatial scales to assess the effects of macroscale (landscape) composition as well as the microscale (nest site) vegetation structure and composition within the broader context. Additionally, we examined how nest survival was influenced by habitat, weather, and temporal variables during 2 breeding seasons.

Study Area

We studied a sample of breeding female prairie-chickens in a 41,930-ha study area in Johnson County in southeastern Nebraska (Figure 1). We selected 2 regions in Johnson County (Figure 1) to trap females based on presence of leks, logistical constraints, and landowner permission. Our study site was characterized by rolling uplands produced from accumulation of glacial till and loess. Soil types in these counties are generally comprised of Wymore-Pawnee soil association (U.S. Department of Agriculture [USDA] 1986). The regional climate is midcontinental with an average annual precipitation of 80.4 cm with the majority of that falling between the months of May and August. Average monthly temperature maximum and minimum were 32° C and −12° C occurring in July and January, respectively (1893–2007, University of Nebraska–Lincoln High Plains Regional Climate Center, http://www.hprcc.unl.edu/). Potential predators of prairie-chicken nests in our study area included coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), domestic dogs and cats, and various species of snakes and other small mammals.

The landscape in the study area was dominated by agricultural development including corn, soybean, and alfalfa production (46%; Figure 1). In addition, 32% of our study landscape was maintained as pasture and rangeland. In 2007, 16,327 ha (40,345 ac; 17%) of Johnson County was enrolled in CRP (Farm Service Agency, USDA, http://www.fsa.usda.gov/Internet/FSA_File/acrescounty012213.xls). Twenty-three percent of our study area was enrolled in CRP (CP-1, nonnative grasses: 11%; CP-2, native grasses: 12%).

Methods

Trapping and Monitoring

We used walk-in traps to capture female prairie-chickens from 2007 to 2008 (Schroeder and Braun 1991). We trapped females on 13 leks (2007: 7, 2008: 10), and leks ranged in size from 15 to 70 males. We selected leks in areas of high CRP density; although we sampled in 2 separate areas (Figure 1), birds could easily disperse between the 2 sampling areas (T. Matthews, University of Nebraska–Lincoln, unpublished data). Once captured, we fitted each female with an 18-g (1.5–2.5% of body mass) necklace style radio transmitter (Model #A3960, Advanced Telemetry Systems, Inc., Isanti, MN), and we released each bird immediately at the capture location. Our animal capture and handling protocols were approved by the University of Nebraska-Lincoln Institutional Animal Care and Use Committee (Protocol #05–02–007).

We estimated the location of each prairie-chicken 5–10 times per week from time of capture to August 1, using a vehicle mounted with a null-peak antenna-receiver with an electronic compass (Gilsdorf et al. 2008). We randomly chose the order of fields in which we tracked individuals to locate each bird at different times of day. We took at least 3 bearings within 10 minutes for each location to minimize movement bias. We took additional bearings until we received an error polygon of less than 1,000 m^2 (approx. 18-m radius). We calculated all Universal Transverse Mercator (UTM) coordinates and associated error polygons in the field via an onboard computer and software (Location of a Signal [LOAS], Ecological Software Solutions, Urnäsch, Switzerland, Version 4.0). We located missing prairie-chickens by systematic ground searches and aerial telemetry. When monitoring indicated a prairie-chicken was nesting (i.e., 2–3 consecutive identical locations),

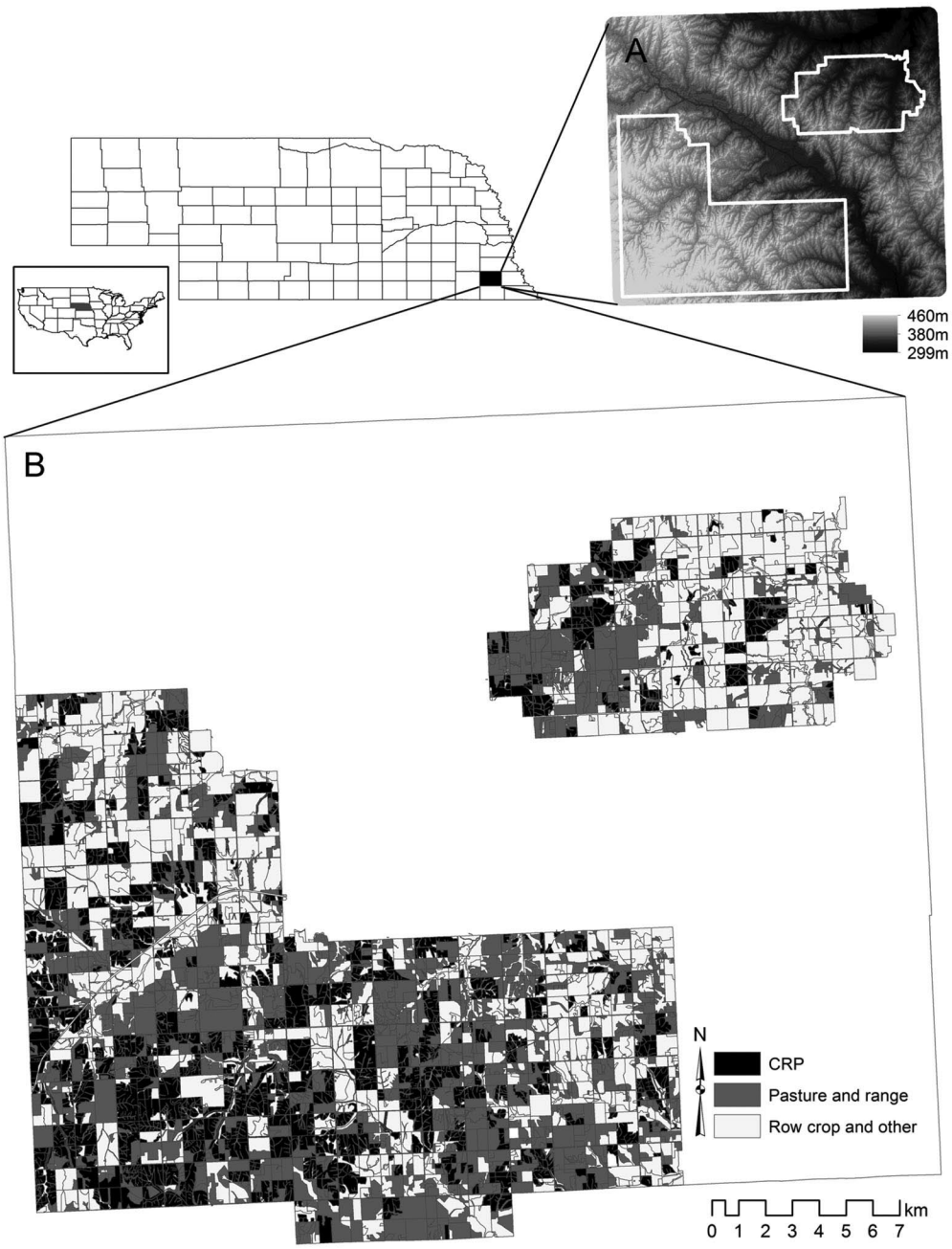

Figure 1. Map of study area in Johnson County, Nebraska (dark inset) in context of elevation (A) and landscape composition (B), including grasslands in Conservation Reserve Program (CRP) contracts, pasture and range, and non-grasslands (row crop and other features, such as farmsteads and water), 2007–2008.

we visually confirmed the nest location. Once locations indicated the female had stopped incubating (i.e., 2–3 locations off nest), we visually inspected the nest to ascertain its fate and the number of eggs that hatched. We did not mark nests, and we only visited the nest at the initial inspection and when the female's radio-telemetry data suggested the nest had hatched or failed (predated or abandoned). We considered nests successful if ≥1 egg hatched.

Nest Habitat Measurement

We evaluated landscape composition by creating a year-specific, vector-based geographic information system (ArcGIS 9.0, ESRI, Redlands, CA) land cover layer. We used visual inspection of aerial photographs, supplemented with ground-truthing throughout the study site as confirmation, to classify our study landscape into 5 land cover types: cropland, grassland, woodland, wetland, and anthropogenic. We further divided grassland cover types into 4 subtypes: 1) warm-season CRP fields, predominately planted to switchgrass *Panicum virgatum*, big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), or sideoats grama *Bouteloua curtipendula*); 2) cool-season CRP fields, dominated by smooth brome and orchard grass (*Dactylis glomerata*); 3) rangelands, i.e. grasslands in a field not enrolled in the CRP program with no history of crop production, and 4) pasturelands, i.e. grasslands in a field not enrolled in the CRP program with a history of crop production.

At each nest site, we estimated the percentage of canopy cover for grasses (grass), forbs (forb), standing litter, and bare ground (bare) using a 1-m diameter sampling hoop (modified from Daubenmire 1959) centered on the nest. We estimated cover on an overlapping basis (Patterson and Best 1996). As such, we allowed total composition to equal ≥100% when vegetation cover classes overlapped (e.g., forb and grass canopy co-mingled) to minimize multicollinearity. We recorded visual obstruction readings (VOR) to the nearest 0.25 dm (Robel et al. 1970). We also used Hawth's Analysis Tools for ArcGIS (Beyer 2004) to select 5 random points in the same field, at which we assessed the vegetation composition and VOR. In addition, we classified each nest site and random point into 3 relative elevation categories (upper, middle, or lower thirds of hill slope), relative to the local elevation context for a particular field using a county-level digital elevation model (DEM; University of Nebraska–Lincoln School of Natural Resources, http://calmit.unl.edu/data_maps.php).

Analysis and Model Selection

We used discrete choice models to assess the probability of female prairie-chickens selecting nesting resources based on characteristics of the resource and available resources (Cooper and Millspaugh 1999). We performed analyses at 2 levels, macrohabitat and microhabitat, and we used the nest as the sample unit (Cooper and Millspaugh 1999, McDonald et al. 2006). We selected the discrete choice approach for its ability to simultaneously consider continuous and categorical types of covariates within a multimodel structure. Also, with discrete choice we were able to customize the composition of the choice set for each location in time and space (Cooper and Millspaugh 1999, McDonald et al. 2006). We used the Cox proportional hazards regression method to develop our macro- and microhabitat discrete-choice models. We constructed our models using the COXPH function located in the survival package of R (R package version 2.31; R Development Core Team 2009). We calculated selection ratios for estimates $\hat{\beta}_i$ using the top model where the selection ratio was defined as e^{β_i}. Selection ratios measure the multiplicative change in relative probability of selection when a covariate is changed by 1 unit and all other covariates are held constant (McDonald et al. 2006). We used 95% confidence intervals to assess strength of effects of covariates, as evidenced from their departure from a null level of 1.0.

We assessed the selection of broad, macrohabitat of nest sites and the finer-scale microhabitat of nests sites in separate analyses because of logical and logistic reasons. First, Jones (2001) suggested that habitat selection studies should be performed in a manner that captures the multiple scales that choices are made by animals. As such, we had interest in the hierarchical nature of selection by prairie-chickens, the notion that a primary level of selection is the type of patch (or field) and the secondary level of selection is the location within a field (microhabitat). Second, this approach also prevented the possibility of creating models with combinations of macro- and microhabitat variables that were more complex than our data allowed.

We created 16 biologically reasonable, a priori models including a null model to evaluate the effects macrohabitat covariates have on habitat selection. Our nest macrohabitat models considered the effect of land cover type on habitat selection. We created a set of covariates for land cover based on our classification of habitat in our study area: cool-season CRP, warm-season CRP, pasture, rangeland, and other habitats (largely anthropogenic and water). We set rangeland as our baseline land cover type. We also considered distance to edge, woodland, and crop in our macrohabitat selection because of the increased potential predator communities and avian perch sites in these areas (Svedarsky et al. 2003, Manzer and Hannon 2005). An edge was classified as any transition in vegetation such as fence rows, tree lines, roads, change in major vegetation type, or other types of boundaries delineating habitat types. We generated 20 random points for each nest within the nest-specific available habitat for comparison with actual nest locations. We defined available habitat as that within a circular area centered on the lek at which the female was caught, with a radius set at the distance between the nest and the lek. We stratified, within all discrete choice models, random locations by their paired use location.

We analyzed the microhabitat selection of nesting prairie-chickens by comparing the microhabitat features of each nest site with the same features taken at the 5 random points in the same field. We addressed concerns of multicollinearity in our analyses by creating a correlation matrix for our composition and structural variables. We were prepared to remove variables if correlation coefficients exceeded 0.6; we did not have to remove any variables to account for multicollinearity (max. $R^2 = 0.4$: grass and bare ground). We created 8 biologically reasonable a priori models, including a null model, using the following sets of covariates: a quadratic model of vegetation composition (% cover; grass + grass^2 + forb + forb^2 + standing litter + standing litter^2), a quadratic model of vegetation structure (VOR + VOR^2 + bare + bare^2), and relative elevation. The models considered were 1) cover, 2) structure, 3) elevation, 4) cover + structure, 5) cover + elevation, 6) structure + elevation, 7) global (structure + cover + elevation), and 8) null model. We hypothesized that vegetation composition could be a key component in nest-habitat selection (Jones 1963, Kobriger 1965), but vegetation structure may become too dense for habitat (as measured by VOR and bare; Hamerstrom et al. 1957, Svedarsky 1979). McKee et al. (1998) also suggested standing residual litter increases nest survival by concealing early nests but an excess (>25%) is detrimental to success. We used quadratic combinations of vegetation structure variables because of the apparent avoidance of extreme vegetation densities as suggested by Buhnerkempe et al. (1984). Lastly, based on personal observations, we hypothesized females would select nest sites near the tops of slopes where relative elevation would allow for the highest survival rates (Götmark et al. 1995).

We followed our assessment of habitat selection with a demographic investigation to answer questions regarding the adaptive nature of choices (Jones 2001). We estimated daily survival of prairie-chicken nests and evaluated time- and site-specific factors that could affect survival using the logistic-exposure method (Shaffer 2004). The logistic-exposure method allows exposure time, or time between visits, to vary. Logistic exposure also allows for time-dependant variables to stay constant within monitoring intervals but vary between intervals (Shaffer 2004). We used this method for nest survival because we generally monitored nests 5 or 6 times per week. We constructed our models using the Shaffer (2004) structure and an adaptation of the logistic regression model in R (Post van der Burg 2005, R Development Core Team 2009). We constructed a set of 16 a priori models of the following groups of covariates: macrohabitat (best model describing selection of macrohabitat), microhabitat (best model describing selection of microhabitat), temporal (ordinal day of initiation [day] + day^2 + nest age [age]), and weather (average daily temperature, average daily precipitation). We hypothesized macro- and microhabitat characteristics selected by prairie-chickens would increase nest survival. Temporal variables, such as hatch date and nest age (Fields et al. 2006), and weather variables (Flanders-Wanner et al. 2004) have been shown to affect nest survival of other galliforms. We estimated date of nest initiation using location data and female movement patterns in concert with egg-laying information from our inspections. We censored any nests that were thought to be abandoned because of our disturbance during monitoring.

We performed model selection using an information-theoretic approach to evaluate a priori models for both nest habitat selection and survival. We ranked each model from most to least support given the data using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). For nest survival, we used effective sample size (n = total number of days samples survived + number of intervals that ended in failure) for the calculation of AIC_c (Rotella et al. 2004). When we hypothesized a nonlinear relationship, we performed a preliminary comparison of a linear model with a nonlinear model before continuing with the global analyses. We computed Akaike weights (ω_i) for each model, where ω_i represents the probability a model is the best approximating model of those considered given the data (Burnham and Anderson 2002). For all model comparisons, we created a confidence set of models with a combined model weight of ≥90% (Burnham and Anderson 2002). We were prepared to select the top model if it was the most parsimonious of the confidence set. Otherwise, we were prepared to model average across the confidence set.

Results

We captured, radio-tagged, and monitored 100 female prairie-chickens (2007: 38; 2008: 62). We located and monitored 90 nests (2007: 36; 2008: 54) in 5 different land cover types. Mean incubation start date pooled over both years was May 17 for first nest attempts and June 5 for second attempts. Mean hatch date was June 12, with an average of 11 eggs hatching/nest. Prairie-chickens nested a mean distance of 1,589 m from the lek at which they were caught (range 168–6,223 m). Thirty-six of 90 nests were successful, 48 nests were depredated, 3 nests were abandoned, and 3 nests were destroyed by mowing. We subsequently removed nests that were mowed from our microhabitat analysis because of the altered vegetation state.

Our discrete-choice analysis of macrohabitat covariates indicated land cover type and distance from woodland were strongly associated with prairie-chicken nesting habitat selection (AIC_c = 430.23, ω_i = 0.52). The second and third best models were included in the 90% confidence set; these models also included distance to crop and distance to edge (Table 1). Because the first model was the most parsimonious, we did not average across the confidence set. The estimate from the top model indicated that a prairie-chicken's relative probability

Table 1. Comparison of competing discrete-choice models for greater prairie-chicken macrohabitat nest selection in southeastern Nebraska, 2007–2008. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c); K is the number of parameters, ΔAIC_c is the difference of each model's AIC_c value from that of the highest ranked model (row 1), and ω_i is the Akaike weight (sum of all weights = 1.00). We considered 16 models including covariates for habitat type and distance (dist) to features and the top 3 models represent the 90% confidence set according to their ω_i

Model	K	AIC_c	ΔAIC_c	ω_i
Habitat + dist to woodland	5	430.23	0.00	0.52
Habitat + dist to woodland + dist to cropland	6	431.99	1.76	0.22
Habitat + dist to woodland + dist to edge	6	432.27	2.04	0.19
Habitat + dist to woodland + dist to cropland + dist to edge	7	434.03	3.80	0.08
Habitat	4	445.35	15.12	0.00
Habitat + dist to edge	5	446.70	16.47	0.00
Habitat + dist to cropland	5	447.60	17.37	0.00
Habitat + dist to cropland + dist to edge	6	448.99	18.76	0.00
Dist to woodland + dist to cropland	2	524.28	94.05	0.00
Dist to woodland + dist to cropland + dist to edge	3	525.53	95.30	0.00
Dist to cropland	1	527.41	97.18	0.00
Dist to woodland + dist to edge	2	528.63	98.40	0.00
Dist to edge	1	535.93	105.70	0.00
Dist to cropland + dist to edge	2	537.84	107.61	0.00
Constant (null model)	0	541.93	111.70	0.00
Dist to woodland	1	543.84	113.61	0.00

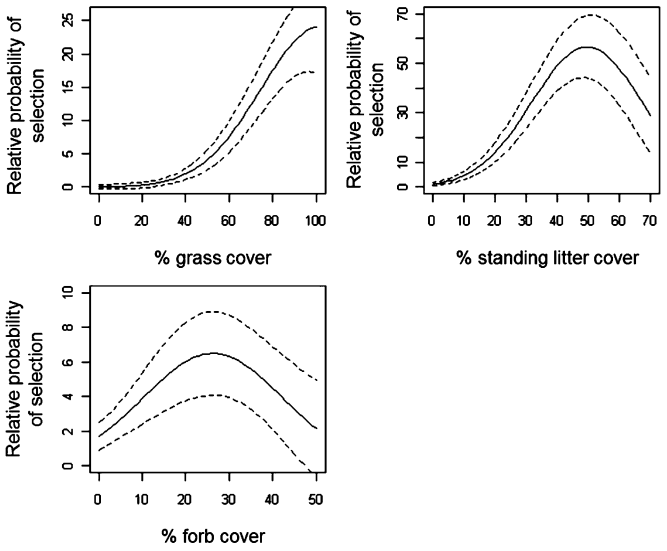

Figure 2. Relative probability of selection, as a function of covariates in the best microhabitat discrete-choice model, by nesting greater prairie-chickens in southeastern Nebraska, 2007–2008. All variables not plotted were held constant at their means to show variation in the covariate of interest. Probabilities were scaled to have maximum values of 1.0, and probabilities are shown only for the range of each covariate in our data (used and random points).

of selecting a nesting location in a cool-season CRP field was 5.70 (95% CI: 2.60–12.48) times greater than rangeland; the probability of selecting a nesting location in warm-season CRP was 5.05 (95% CI: 2.17–11.72) times greater than rangeland. Prairie-chickens were 9.52 (95% CI: 2.02–45.45) times less likely to nest in land cover types classified as other habitat than rangeland. The top model also indicated the relative probability of a prairie-chicken selecting a point in a field, with land cover types held constant, increased 20% (95% CI: 10–30%) with each 100-m increase of distance from woodland.

The top model for predicting microhabitat selection of nesting prairie-chickens included vegetation composition and elevation (AIC_c = 155.13, ω_i = 0.9; second-best model: global model, ΔAIC_c = 4.1). Our preliminary analyses supported the inclusion of nonlinear terms that we had hypothesized ($\Delta AIC_{c\ linear} > 2.0$). The composition and elevation model was the only model in the 90% confidence set. Prairie-chickens selected nest sites in the upper topographic strata in fields 5.78 (95% CI: 2.04–17.42) times more than the lowest topographic strata and 3.64 (95% CI: 1.59–7.26) times more than the middle topographic strata. We also found a relationship between nest microhabitat selection and percentage of cover at the nest of grasses, standing litter, and forbs. Selection for a location as a nest site increased as percent cover of grass, standing litter, and forbs increased, within maxima for selection of sites occurring at 51% standing litter and 21% forb cover (Figure 2).

Variation in daily nest survival (DNS) was best explained by 2 models, which both indicated survival was a function of macrohabitat, microhabitat, and time-specific covariates with the second best model also including weather variables (Table 2). The top 2 models accounted for ≥90% of the ω_i; we selected the most parsimonious of these. Survival tended to be greater in both cool-season (DNS = 0.968, 95% CI: 0.919–0.988; 25-day nest success: 0.443, 95% CI: 0.095–0.792) and warm-season (DNS = 0.975, 95% CI: 0.930–0.991; 25-day: 0.536, 95% CI: 0.177–0.894) CRP fields than rangeland (DNS = 0.865, 95% CI: 0.624–0.961; 25-day: 0.026, 95% CI: 0.014–0.038). Nest survival was also affected by the composition of vegetation at the nest site, including effects of grass, standing litter, and forb cover (Table 3, Figure 3). Nest survival in-

Table 2. Comparison of competing logistic-exposure models for greater prairie-chicken daily nest survival in southeastern Nebraska, 2007–2008. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c); *K* is the number of parameters, ΔAIC_c is the difference of each model's AIC_c value from that of the highest ranked model (row 1), and ω_i is the Akaike weight (sum of all weights = 1.00). We considered 16 models; the top 2 models represent the 90% confidence set according to their ω_i

Models	*K*	AIC_c	ΔAIC_c	ω_i
Macrohabitat[a] + microhabitat[b] + temporal[c]	17	336.561	0.000	0.724
Macrohabitat + microhabitat + weather[d] + temporal	19	338.962	2.401	0.218
Microhabitat + temporal	12	343.065	6.504	0.028
Microhabitat + weather + temporal	14	345.821	9.260	0.007
Temporal	4	346.279	9.718	0.006
Macrohabitat + microhabitat	14	346.324	9.763	0.005
Microhabitat	9	347.567	1.006	0.003
Macrohabitat + microhabitat + weather	16	347.581	1.020	0.003
Macrohabitat + temporal	9	348.288	11.728	0.002
Weather + temporal	6	348.975	12.414	0.001
Microhabitat + weather	11	349.653	13.092	0.001
Macrohabitat + weather + temporal	11	350.324	13.763	0.001
Constant	1	351.961	15.400	0.000
Weather	3	354.316	17.755	0.000
Macrohabitat	6	355.956	19.395	0.000
Macrohabitat + weather	8	357.368	20.807	0.000

a. Macrohabitat covariate set: land cover type + distance to woodland.
b. Microhabitat covariate set: % grass cover + % forb cover + % standing litter cover + relative elevation.
c. Temporal covariate set: ordinal day (of nest initiation) + ordinal day^2 + nest age.
d. Weather covariate set: daily precipitation + daily temperature.

Table 3. Coefficient (β) estimates and 95% confidence intervals for covariates in the top model predicting daily nest survival of greater prairie-chicken nests in southeastern Nebraska, 2007–2008

Covariate	β estimate	95% CI	
		Lower	Upper
Intercept	−42.900	−70.771	−15.029
Habitat			
Cool-season CRP[a]	1.555	0.353	2.757
Other	−0.198	−2.08	1.685
Pasture	−0.416	−1.619	0.788
Warm-season CRP	1.823	0.371	3.275
Distance to woodland	0.001	0.000	0.003
% Grass cover	−0.049	−0.126	0.028
% Grass cover^2	0.001	0.001[b]	0.001[b]
% Standing litter cover	0.046	−0.011	0.103
% Standing litter cover^2	−0.001	−0.002	−0.001
% Forb cover	−0.07	−0.212	0.073
% Forb cover^2	0.006	0.001	0.012
Elevation			
Bottom	0.381	−1.373	2.135
Mid	0.788	0.054	1.523
Ordinal day	0.619	0.229	1.009
Ordinal day^2	−0.002	−0.003	−0.001
Nest age	−0.073	−0.125	−0.021

a. CRP = Conservation Reserve Program
b. Rounded.

creased as grass and forb cover increased, and our data suggest nests with forb cover of greater than 25% are especially likely to be successful. Nest survival tended to decline when cover of standing litter was more than 25%. Nest survival decreased as nests aged, and was at its maximum when prairie-chickens started incubating nests on 28 May (Table 3, Figure 3).

Discussion

Our study suggests both cool- and warm-season CRP grasslands provide better quality nesting habitat for prairie-chickens than other grassland types in southeastern Nebraska, which emphasizes the potential for federal land policy to positively affect wildlife populations of conservation concern. Seventy-five percent of radio-marked prairie-chickens in our sample nested in CRP fields, although this type of land cover only represented 28% of the available land cover. Similarly, 31 nests (apparent success: 45.6%) hatched in CRP fields with only 5 (22.7%) surviving in other grassland types. Svedarsky et al. (2003) also reported selection of CRP fields for nesting by prairie-chickens, but the CRP fields were planted to smooth brome (*B. inermus*) or other cool-season grass mixes. To our knowledge, our study is the first to show that prairie-chickens prefer undisturbed native warm-season CRP fields over grazed or hayed rangeland and pastures (Table 2). Some differences exist between the warm-season CRP fields in our study site and typical warm-season CRP fields. First, the majority of warm-season CRP fields in our study area were severely encroached by smooth brome. Although warm season fields have the potential to produce vegetation that is too tall and dense for nesting prairie-chickens (Hamerstrom et al. 1957, Westemeier 1973), we observed that warm-season CRP fields on our study site had not developed full density by the time nesting was initiated; this may contrast with nesting conditions in prairie-chicken habitat in more southern locations. In warm-season CRP fields on our study site, dead, standing vegetation from the previous year probably provided critical cover (Svedarsky et al. 2003), whereas we noted that this was lacking in pasture and rangelands. Similar patterns of habitat characteristics and use by

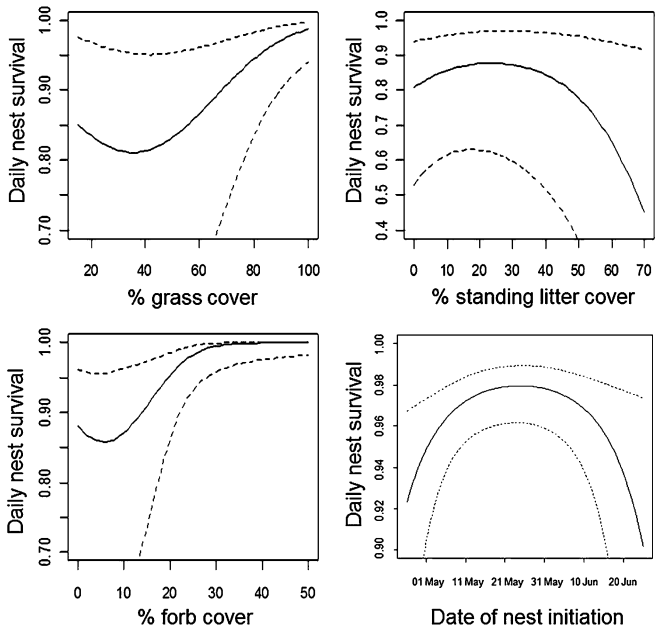

Figure 3. Daily nest survival, as a function of covariates in the best logistic-exposure model, by greater prairie-chickens in southeastern Nebraska, 2007–2008. All covariates not plotted were held constant at their means to show variation in the covariate of interest, and daily survival is shown only for the range of each covariate in our sample of nests.

prairie-chickens were reported by McNew et al. 2011a, 2011b) and Patten et al. (2007).

In addition to responding to the type of land cover, prairie-chickens selected nest sites further from woodlands than random points. This may be in response to the high abundance of mammalian and avian predators along wooded corridors (Svedarsky et al. 2003, Manzer and Hannon 2005). Some rangeland and pastureland may have been unsuitable for nesting because of the advancement of woody cover, mainly eastern red cedar (*Juniperus virginiana*). Trees can provide perch sites for many avian predators that use visual cues to find prey (Manzer and Hannon 2005). Encroachment of woody cover in CRP fields may not have been as severe because of the relatively young age (<20 yr) of the grasslands on our study area. If true, this suggests that the increased suitability of CRP fields for prairie-chickens is ephemeral and will not persist without efforts to control woody cover. Briggs et al. (2002) suggested that cedar could degrade native prairie in as little as 5–7 years and turn native grasslands into a cedar forest in <25 years. Future studies could evaluate this potential explanation for the selection of CRP fields by planning for a balanced sample of nests among types of land covers and testing for an interaction between land cover and distance to woodland. Inferences from our results should be assessed in the context of the spatial and temporal scope of our study.

Habitat selection of nest sites within fields in our study was strongly associated with vegetation composition, rather than structure, which is similar to the results of McKee et al. (1998). The lack of a response to structure, as measured by VOR, conflicts with the results of Hamerstrom et al. (1957), Tester and Marshall (1962), Jones (1963), and Buhnerkempe et al. (1984). On our study area, grass cover at the nest site may provide concealment from avian predators, as females tended to avoid sites in our study area with low levels of grass cover. The influence of vegetation structure on nest site selection in our study may have been limited by the relatively homogenous vegetation height within fields, which was especially apparent in CRP fields. Prairie-chickens selected a narrow range of forb cover and standing litter cover. Females were twice as likely to select nesting locations that contained 25% forb cover than areas with 10% or 40% cover (Figure 2). Forbs, mainly alfalfa (*Medicago sativa*) and red clover (*Trifolium pratens*), found in this moderate density provide the needed overhead and lateral cover. As the basal stem densities of these plants increase, the vegetation may hinder movements and associated anti-predator behavior of prairie-chickens. Nest survival did not decrease at high levels of forb cover, which suggests females may avoid high levels of forb cover to maximize their own survival, rather than their nests. The flush response of females when encountering a predator may also help explain the selection of the top third of a field in elevation for nesting (Table 2). Females may increase their nest success by selecting a nest site with a good view of their surroundings (Götmark et al. 1995). Hens also may have selected upper elevations in fields to avoid high nest predation near edges (Clark et al. 1999). However, we found no advantage of upper elevation on nest survival. Thus, prairie-chickens may find advantage to lifetime fitness by selecting areas of upper elevation, usually hilltops and ridges, which may provide a better vantage point to survey the surrounding area and to be able to flush when approached by predators (Westemeier 1973).

During our study, CRP grasslands provided nest success rates (apparent nest success, all CRP: 46.9%; 25-day nest survival in cool-season CRP: 44.3%, warm-season CRP: 53.6%; Table 3) similar to the 47.9% found in other regions (Peterson and Silvy 1996) and near the minimum of 50% apparent nest success suggested by Westemeier (1973) for a stable population. This suggests that both warm- and cool-season CRP grasslands provide adequate surrogate grasslands for prairie-chicken nesting and are not the cause of the low juvenile:adult ratios (approx. 0.9) observed in harvested birds in and around our study area reported by Powell et al. (2011). Because we found the majority (approx. 75%) of the nests in CRP fields and they had high rates of nest survival, we attribute the low production to low brood survival (Matthews et al. 2011, Schole et al. 2011). Prairie-chickens nesting in non-CRP grasslands and agriculture lands experienced a significant decrease in nest survival (Table 3), with an apparent nest success of 21.7%. The disparity in nest survival between CRP and non-CRP grasslands is likely due to the increased vegetative cover, both growing and dead, in the undisturbed CRP grasslands. Morrow (1987) suggested managers should use grazing strategies that allow portions of the landscape to produce enough residual cover for the subsequent year's nests for Attwater's prairie-chickens (*Tympanuchus cupido attwateri*).

Grass and forb cover were also predictors of nest success for prairie-chickens (Tables 2 and 3) with, generally, a positive relationship between DNS and cover (Figure 3). Prairie-chickens tended to select nest sites with more grass cover (Figure 2), and sites with more grass cover tended to have greater nest survival (Figure 3). McKee et al. (1998) also found forb and grass cover to influence nest success. However, unlike McKee et al. (1998), we did not find horizontal litter cover to affect nest success. Instead, our data suggest that standing (vertical) litter cover of more than 25% may have a deleterious effect (Figure 3). Nests in sites with more grass and forb components may benefit from concealment from predators, and grass and forbs may also provide shelter from adverse weather. Standing litter may also serve this purpose. The decrease in daily survival of nests with >25% standing litter may be caused by a decrease in other influential vegetative components. McKee et al. (1998) found a negative relation between litter cover and grass cover. Excessive litter can delay new grass growth and decrease cover for nesting (Westemeier 1973). An increased amount of litter has also been linked with an increase in small mammal populations and, in turn, to an increase in predator activity in the area (Svedarsky 1979).

Temporal effects (i.e., nest initiation date and nest age) had a large influence on nest survival and were included in the top 5 models in our analysis (Table 2). The decrease in nest survival as nests age has been shown in other prairie grouse and was attributed to an increase in mam-

malian predation caused by the increased scent left by the female and gas exchange from eggs (Fields et al. 2006). As a nest ages, cues that lead to nest discovery by a predator, such as parental movements near the nest (Fontaine and Martin 2006), accumulate (Grant et al. 2005). In contrast, Coates and Delehanty (2010) reported that survival increased as greater sage-grouse (*Centrocercus urophasianus*) nests aged. Evidence from videography suggested that nests of sage-grouse females employing riskier behavior were found quickly by ravens (*Corvus corax*) using visual cues (Coates et al. 2008). The contrast with our study, with regard to age-related nest survival, may be explained by the cues used by the contrasting predator communities as ravens were not present at our study site.

The quadratic effect of initiation date on nest success (Figure 3) was most likely caused by a variety of variables. Nests initiated too early in the season would not have adequate growth from the current year's vegetation to hide the nests from predators (reviewed by Evans 2004). McNew et al. 2011a) reported that prairie-chickens in Kansas delayed nest initiation by more than a week in areas lacking suitable nesting cover. Decreased nest survival early in the season because of the phenology of vegetation growth may be compounded in pasturelands and rangelands because of the lack of standing litter cover (McNew et al. 2011a). Undisturbed CRP fields may provide the only suitable alternative for the early nesting birds. Nest survival may peak as cool-season grasses begin to provide cover, and as alternative prey items, such as small rodents, become more numerous (French et al. 1976, reviewed by Evans 2004). Fields et al. (2006) also found nest survival of lesser prairie-chickens decreased as the season progressed and attributed it to a decrease in female condition and increased humidity. We note that the date of maximum nest survival (Figure 3) occurred 1 week after the peak in nest initiation on our study site (Matthews 2009). The increase in prey opportunities for nest predators may swamp predation efforts and increase survival for the individual (Krebs and Davies 1984) because of the relatively low densities of prairie-chickens.

We had a priori reasons to consider nonlinear responses for many characteristics of nest sites. Our results should be considered in the context of our approach to model comparison. We constructed models with groups of covariates, rather than assessing individual covariates, to reduce the number of models under consideration and to evaluate broader hypotheses. As such, covariates of minor importance could be carried along by the strength of covariates of major importance. However, we visually reviewed the effects of covariates (Figures 2 and 3) to assess their relevance. Tradeoffs exist among methods of model construction when multimodel inference is used to examine complex systems. Rehme et al. (2011) found large variation in methods of interpretation and presentation, especially with regard to model-averaging. We provide confidence intervals (Figures 2 and 3) so that the level of uncertainty from the process of model selection and the potential for simpler linear effects can be evaluated by the reader. To wit, we have refrained from discussing minima or maxima in our nest survival analyses because of the uncertainty suggested in those trends (Figure 3).

Management Implications

Our research suggests that efforts to manage the population of prairie-chickens in southeastern Nebraska should focus on establishing new grasslands and maintaining key vegetation attributes at optimal levels, especially in CRP fields. The CRP fields, both native warm-season and cool-season plantings, appear to have provided critical nesting habitat in our study area. In addition, our research would support the use of methods, such as controlled burning, interseeding of forbs, tree removal, and prescribed grazing to produce grasslands with favorable herbaceous heterogeneity and density. Our study further suggests that management efforts should be especially focused on grasslands in areas near or on ridge tops to improve nest habitat suitability and nest survival. Private land consultants often encourage the development of CRP acres as stream buffers for soil erosion, but the emphasis on stream buffers may lead to missed opportunities to increase productivity by providing habitat on ridge tops, away from riparian woodlands. In sum, we provide considerable evidence for the effectiveness of landscape-level management for prairie-chickens through federal farm programs such as CRP. Our data suggest that farm policy can be used to support this species of conservation need through the addition of CRP and similar grasslands to landscapes.

Acknowledgments — We acknowledge M. Remund and B. Goracke, Nebraska Game and Parks Commission (NGPC) biologists who supported our project at the Osage Wildlife Management Area. The NGPC funded our research and provided equipment, housing, and logistical support. A portion of this research was funded by a State Wildlife Grant (T-55) administered through NGPC, and Nebraska Pheasants Forever provided equipment. S. Huber, A. Schole, and S. Groepper provided valuable field assistance. The School of Natural Resources provided computer and office space for TWM, AJT, and LAP. LAP was supported by Polytechnic of Namibia and a Fulbright award through the U.S. State Department during a professional development leave when this paper was written. An earlier version of this manuscript was improved by comments from 2 reviewers for *Journal of Wildlife Management* and its Associate Editor, Peter Coates. This research was supported by Hatch Act funds through the University of Nebraska Agricultural Research Division, Lincoln, Nebraska.

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